Plant-insect interactions in the Selandian (Early Paleocene) Gelinden Fossil Flora (Belgium) and what they mean for the ecosystems after the Cretaceous-Paleogene mass extinction

Author links open overlay panelRaphaël Zambon [a], Julien Denayer [a], Cyrille Prestianni [a b]

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Abstract

This study aims to quantify the intensity and diversity of plant-insect associations observed in the fossil assemblage of Gelinden, Limburg, Belgium. The site yields a rich collection of well-preserved plant remains, mainly leaves, from a Paleocene European temperate forest. The 780 specimens presented here were scanned using standardized morphotype systems for any trace of damage. This raw data was then used to quantify the intensity and diversity of interactions in the Gelinden flora. This material showed an impressive richness of interactions, contrasting with the poor North American sites covering the period that followed the Cretaceous-Paleogene extinction. Both hosts and interaction types observed at Gelinden are two to three times more abundant than in most American floras, in raw numbers and leaf area affected. This is coherent with what has been observed in the few other studies conducted in Europe, South America and Antarctica, pointing toward more regionalized effects of the extinction than previously assumed based on American findings. This greater richness implies that these sites were either less affected or quicker to recover from the Cretaceous/Paleogene extinction, questioning its global impact, at least on the lower levels of the food web, as discussed in the following paper.

Introduction

Plant-insect interactions are among the most important relationships in the living world, as they link two of the most abundant lineages of organisms, both in terms of biodiversity and biomass (Labandeira and Currano, 2013). This importance is reflected in the multiplicity of their interactions, ranging from mutualism such as pollination, to herbivory (Labandeira, 2005, Labandeira, 2006). The interactions, particularly those based on herbivory, can leave traces in the fossil record (Labandeira, 1998, Labandeira, 2007). Studying them gives us crucial information on the evolution through time and space of these associations and their mechanics, which are still relevant in the present time (Labandeira, 2005, Labandeira, 2006; Liu et al., 2015). Being at the base of the food chain of most ecosystems, they are directly impacted by changes in climate, such as rises in temperature and atmospheric CO_2 associated with modern global change (Currano et al., 2016; DeLucia et al., 2012). Studying these interactions in deep time and their evolution in the face of ancient global changes gives us precious clues to understand and anticipate their modern and future reactions (Wilf and Labandeira, 1999; Wilf et al., 2001).

The Paleocene is a particularly interesting period from this point of view, as it directly follows the cataclysmic events of the Cretaceous-Paleogene (K-Pg) extinction and ends with the sudden warming of the Paleocene-Eocene Thermal Maximum (PETM), changes which reflect on plant-insect associations (Currano et al., 2010; Tanrattana et al., 2020). However, whereas Paleocene plant-insect associations have already received a particular interest with the development of the broader

discipline in the last 30 years, most of these studies have focused on North American floras (Currano et al., 2008; Wilf et al., 2006; Wilf, 2008 and reference therein). However, the few similar studies on South American and European sites yielded floras comparatively richer both in plant hosts and interaction traces, revealing distinct dynamics compared to their North American equivalents, in particular when it comes to the diversity of insect-mediated damages (Carvalho et al., 2021; Donovan et al., 2017, Donovan et al., 2018; Giraldo et al., 2021; Wappler et al., 2009; Wappler and Denk, 2011). They lack the clues pointing to a steep decline in plant and interaction richness following the K-Pg extinction or a slow recovery culminating at the PETM, as is observed in North America. On the contrary, the European and South American sites seem to have been far less affected by both events, a tendency that could be explained by their geographical location (Wappler et al., 2009).

This study aims at investigating the unexpectedly diverse traces of damage present in the fossil flora from the Selandian Gelinden site (Belgium) (de Saporta, 1873, de Saporta and Marion, 1878; Tanrattana et al., 2020). The point is to provide a basis of data usable for comparison of sites of similar age and nature and, therefore to lead to a better understanding of the dynamics of plant-insect interactions during the Paleocene of Europe and in the rest of the world.

Section snippets

Geological context

The Gelinden site is located in eastern Belgium, near the town of Heers, between Tongeren, Waremme and Sint-Truiden (WGS84 5°15’55.703”E 50°45’24.926”N). It belongs to the southern margin of the Cenozoic North Sea Basin, where the lower Paleogene deposits rest uncomfortably on Upper Cretaceous limestones and chalks (Fig. 1).

The specimens presented in this study were collected in the Gelinden Member of the Heers Formation (Dreesen et al., 1998), which gave its name to the *Heersien*, a disused

Material

No newly collected material was studied during this work. All specimens presented here come from three collections housed at the Royal Belgian Institute of Natural Sciences, the University of Liège and the Catholic University of Leuven (See Table 1 for the composition of each collection). They were collected in the nineteenth century by the workers of the Gelinden quarry. The lack of expertise of the collectors might have resulted in a non-negligible selective bias, particularly toward

Leaf morphotypes

A total of 35 leaf morphotypes were identified, 33 of which correspond to species initially described by de Saporta, 1873, de Saporta et al., 1878. Most morphotypes correspond to angiosperms taxa. The exceptions are GL-17 (*Chamaecyparis belgica*, a conifer) and GL-31 (unidentified cycad, possibly *Zamites sp.*), neither of which presented damage traces. Morphotypes GL-02 and GL-10, respectively, correspond to *Dryophyllum dewalquei* and *Dewalquea gelindenensis*. They stand out as particularly

Comparison with other Paleocene floras

Whereas plant-arthropod interactions study is a relatively new field in paleontology, numerous studies have already been conducted on the subject, based on assemblages dating from the Lower Devonian to the late Neogene (Labandeira and Currano, 2013). The Paleocene in particular has been one of the most sampled eras (Currano et al., 2021). However, most studied Paleocene localities are

located in the United States (Azevedo Schmidt et al., 2019; Wilf et al., 2006; Wilf, 2008), with only a few

Conclusion

The Gelinden assemblage has revealed a surprisingly rich array of damage traces, indicative of an ecosystem with a high diversity of plant-insect interactions. These data help us better understand the ecosystems of that time and their reaction to changes. The diversity at Gelinden strengthens the hypothesis according to which ecosystems located further away from the Chixculub impact were less affected by and recovered faster from the Cretaceous-Paleogene mass extinction. Gelinden is

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The following are the supplementary data related to this article.

. Raw data from the Gelinden assemblage.

. Collection of supplementary plots describing the proportion of damaged specimens and morphotypes abundance, with comparisons to Menat.

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